

**Taxonomic Descriptions of the Immature Stages of  
the Parasitic Bee, *Stelis* (*Odontostelis*)  
*bilineolata* (Spinola)  
(Hymenoptera: Apoidea: Megachilidae)**

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**Abstract:** This paper describes taxonomically the first and last larval instars and the pupa of this species. It compares the mature larva with that of other known *Stelis*, and although there is considerable intrageneric variation, the larvae of *Stelis* cannot be distinguished as a group from those of other Megachilidae. The pupa of this species agrees in most respects with those of other megachilid bees.

The purpose of this paper is to record details of the anatomy of the first and last larval instars and of the pupa of *Stelis* (*Odontostelis*) *bilineolata* (Spinola) for future taxonomic and evolutionary consideration. Although the mature larvae of a number of species of *Stelis* have been described before, this is believed to be the first account of the mature larva of the Neotropical subgenus *Odontostelis* and to be the first formal description of the pupa and first instar of any *Stelis*.<sup>2</sup> In an accompanying paper Bennett (1966) discusses the biology of this parasitic bee which depredates the nest of the brilliant green apid bee, *Euglossa cordata* (Linnaeus).

**Acknowledgment**

I would like to thank Dr. Fred D. Bennett, Entomologist-in-Charge, West Indian Station, Commonwealth Institute of Biological Control, Curepe, Trinidad, the West Indies, for the gift of specimens used in this study. Because of his energetic efforts in collecting the immature stages of Trinidadian bees, we are at long last gaining an understanding of the larvae and pupae of many Neotropical apoids.

MATURE LARVA

(Figs. 1-8)

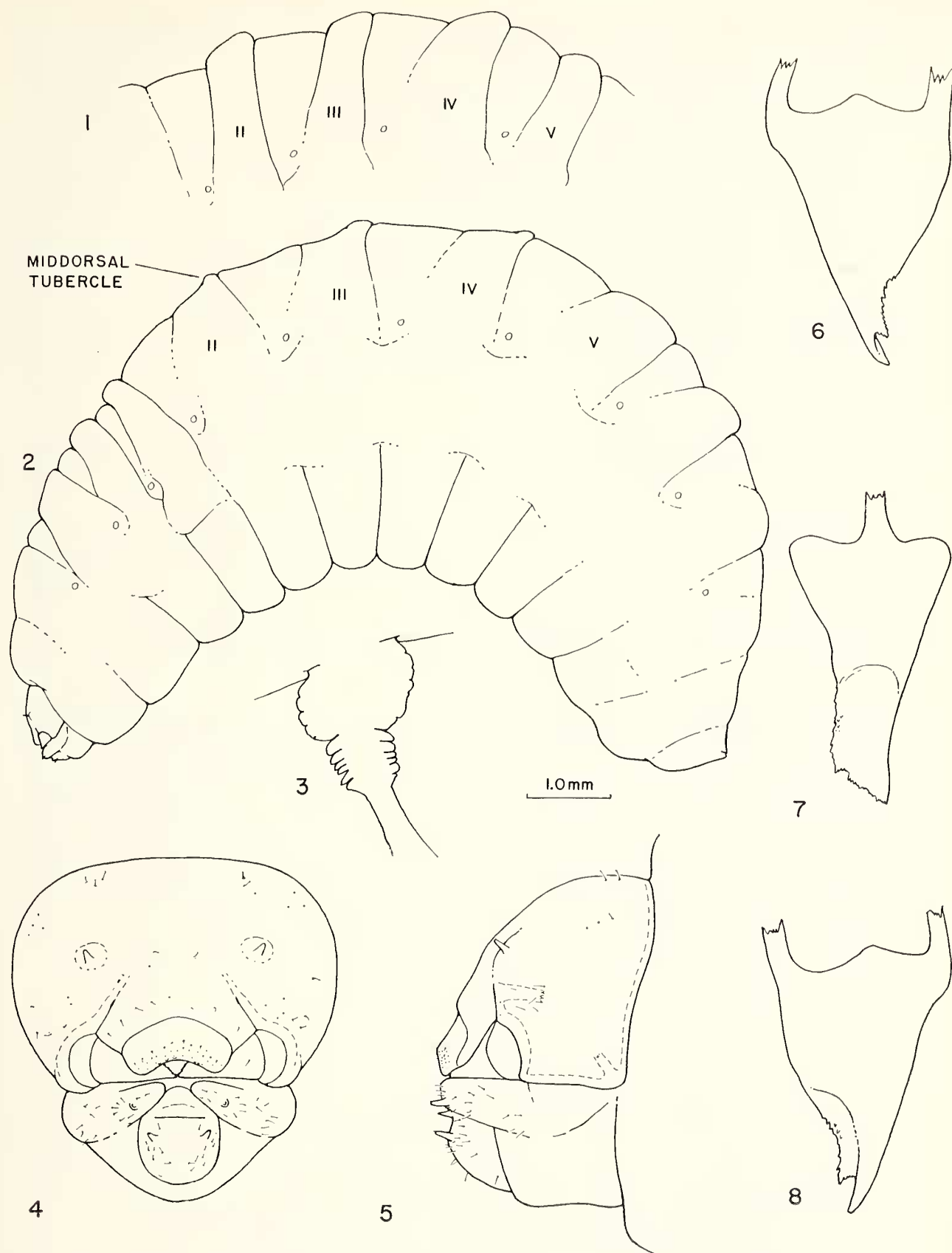
LENGTH: 10.0 mm.

HEAD (Figs. 4, 5): Integument with numerous scattered long setae but without spicules except for faint ones on dorsal surface of maxilla; labrum, dorsal mandibular articulation, mandibular apex, hypostomal ridge, cardo, and stipes pigmented; prementum with narrow pigmented sclerite extending from below level of palpus dorsad and laterad of palpus above salivary lips and down other side, thereby circumscribing arc of approximately 270 degrees; antennal papillae and palpi also somewhat pigmented. Tentorium well developed except dorsal arms very short; posterior pits conspicuous and normal in position, i.e., at junctures of posterior thickening and hypostomal ridges; posterior thickening of head capsule and

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<sup>2</sup> The literature search for this project was accomplished with the assistance of the Bibliography of Apoid Biology which is under the direction of Dr. C. D. Michener, University of Kansas, Lawrence.



FIGS. 1-8. Last larval instar of *Stelis (Odontostelis) bilineolata* (Spinola). 1. Part of abdominal dorsum, lateral view. 2. Postdefecating larva, lateral view. 3. Spiracle. 4-5. Head, frontal and lateral views. 6-8. Mandible, dorsal, adoral, and ventral views. Scale refers to Figs 1 and 2.

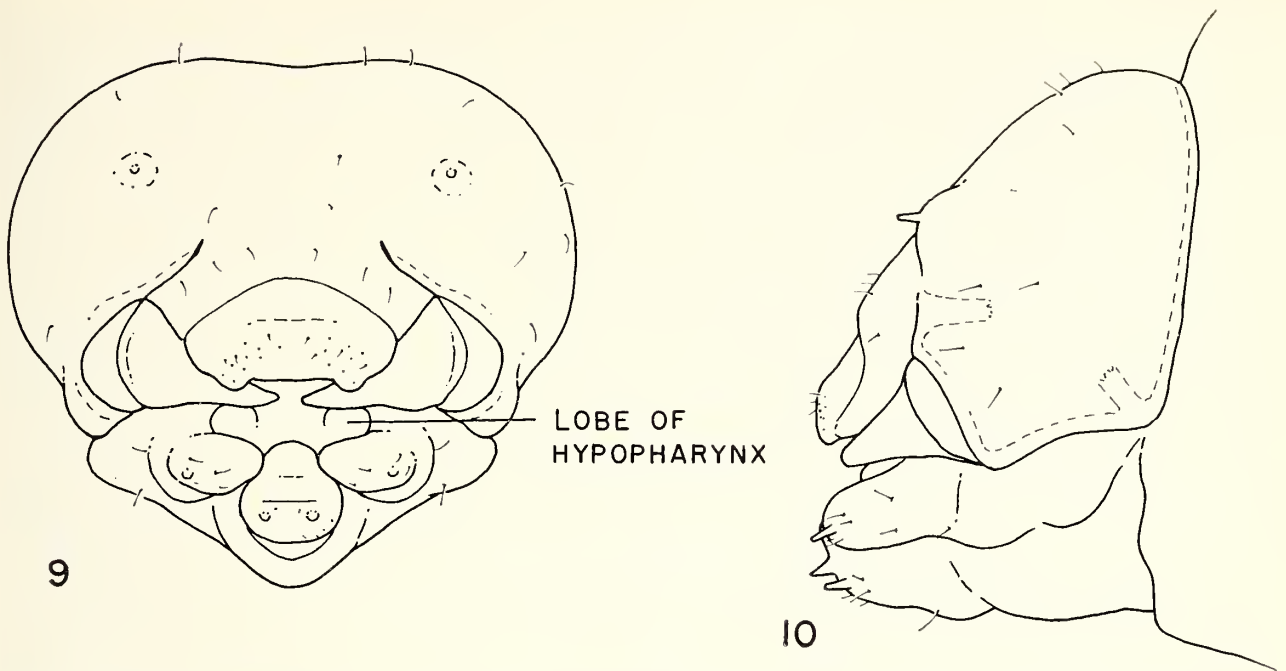
hypostomal ridge well developed; pleurostomal ridge moderately wide but fairly thin; epistomal ridge well developed laterad of anterior tentorial pits and extending dorsomedially short distance mesiad of pits before disappearing; longitudinal thickening of head capsule, cleavage lines, and parietal bands not evident. Antennal papilla elongate, being approximately twice as long as basal diameter; papilla arising from only very low prominence. Labral apex broadly emarginate apically and without tubercles. Mandible (Figs. 6-8) apically bidentate with ventral tooth longer; margin between teeth finely but sharply dentate; mandible with apical concavity limited basally by transverse ridge; dorsal apical inner edge finely but sharply dentate; ventral edge smooth; cusp not dentate. Maxilla with apex produced adorally; galea absent; palpus elongate, being as long as but slightly thinner than antennal papilla; cardo and stipes sclerotic. Labrum projecting, divided into prementum and postmentum, and bearing salivary opening at apex; salivary opening a transverse slit with projecting lips; labial palpi as long as maxillary palpi; hypopharynx with prominent lobe on each side next to maxilla.

**BODY:** Form (Fig. 2) of postdefecating larva robust and with most segments having distinct intrasegmental lines; low middorsal tubercles present on posterior margin of abdominal segments II to IV; tubercles not evident when these segments telescoped (Fig. 1); ventrolateral tubercles present but not pronounced. Integument of postdefecating form soft; dorsal surface more or less evenly covered with fine light setae (not shown in illustrations); ventral surface with setae sparser. Spiracular atrium (Fig. 3) with short dentate ridges; atrium projecting above body wall and with rim; peritreme present; primary tracheal opening with collar; subatrium moderately short. Tenth abdominal segment short; anus situated dorsally.

**MATERIAL STUDIED:** Two postdefecating larvae, Curepe, Trinidad, West Indies, February 10, 1965, from cells of *Euglossa cordata* (Linnaeus) (F. D. Bennett).

While preparing the preceding description, I compared in detail the larva of *bilineolata* with the mature larva of *Stelis* (*Microstelis*) *lateralis* Cresson, kindly loaned by Dr. Charles D. Michener. Drawings of the head of *lateralis* (Figs. 9, 10) are presented here to supplement those provided by Michener (1953) with his description of the last instar. The larva of *lateralis* differs from that of *bilineolata* in a number of ways: *S. lateralis* is much smaller, being only 6.0 mm long. Its head is somewhat differently shaped as seen in lateral view, and there is a strong indentation along the median line of the head capsule. The labrum is not so distinctly emarginate apically, and there are two low labral tubercles. The mandibles are remarkably different, as discussed below. The labiomaxillary region is much more strongly produced. Each maxilla is strongly constricted below the base of the mandible whereas in *bilineolata* there is no such modification. The sclerites of the prementum appear to be quite different from those of *bilineolata*; there is no dorsal sclerotic bridge above the salivary opening but the sclerites are joined ventrally behind the palpi and form a wide, faint plate occupying most of the ventral surface of the prementum. The prementum in frontal view is narrower, and the two lobes of the hypopharynx are more pronounced. The middorsal tubercles (Michener, 1953, fig. 114) of the body are more conspicuous and the body setae less numerous. The spiracle (Michener,





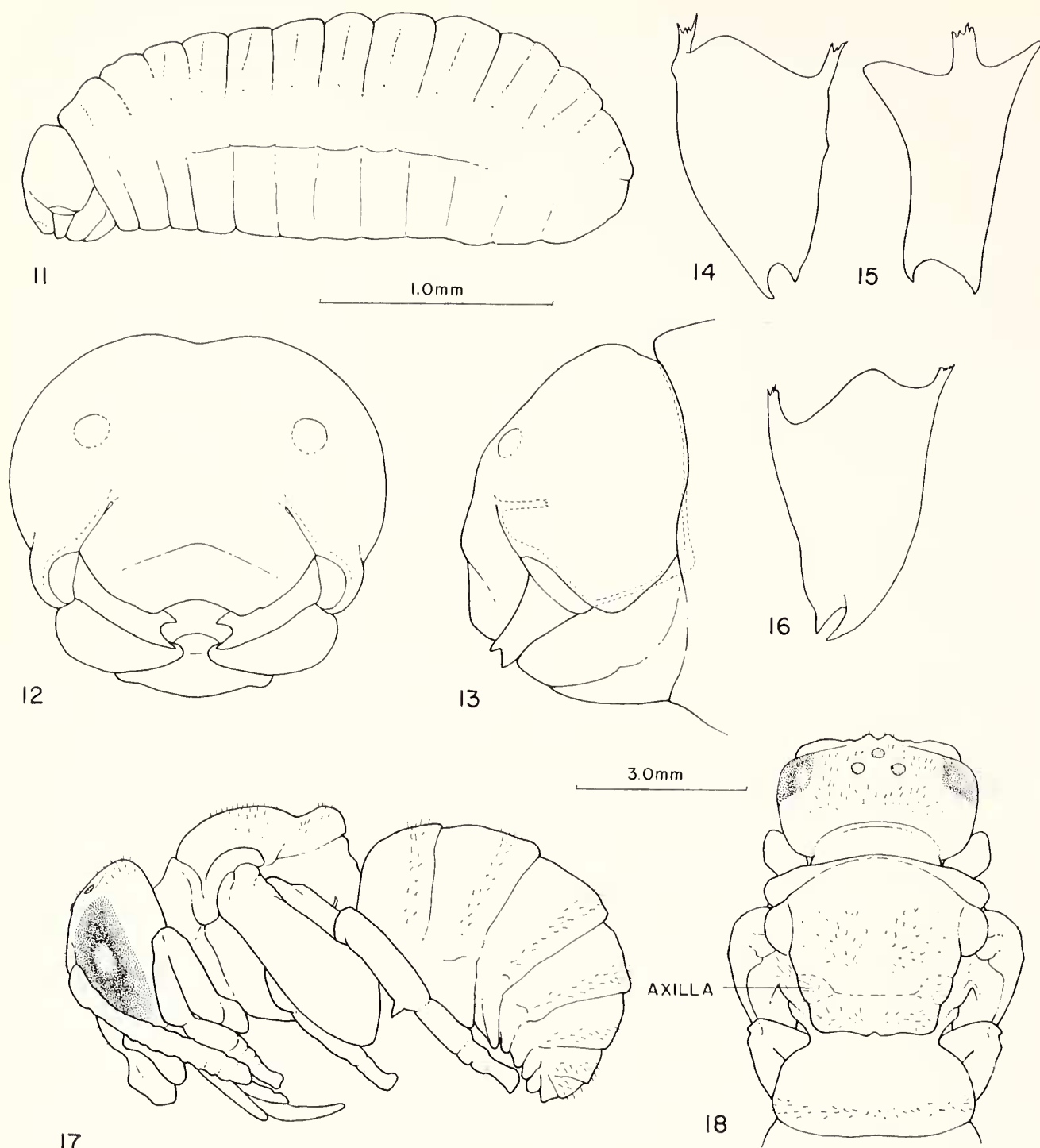
FIGS. 9-10. Head of mature larva of *Stelis* (*Microstelis*) *lateralis* Cresson, frontal and lateral views.

1953, fig. 118) apparently possesses longer atrial spines and a relatively longer subatrium.

Comparisons can also be made, in a general way, with the larvae of a number of other *Stelis* on the basis of the following descriptions in the literature: *Stelis* (*Stelidomorpha*) *nasuta* (Latreille) (Maneval, 1937), (*Stelis*) *minuta* Lepeletier and Serville (Enslin, 1925), (*Stelis*) *ornatula* (Klug) (Micheli, 1935). The resulting conclusions are that the known larvae of *Stelis* possess the megachilid characters presented by Michener (1953), and that no feature or set of features is evident at this time that will enable *Stelis*, as a group, to be distinguished from other Megachilidae.<sup>3</sup>

It seems evident from all studies of *Stelis* larvae that the species differ one from the other to a considerable extent. However, an examination of *bilineolata* reveals that a few apparent dissimilarities may not be so pronounced as previously judged. The extent of expression of the middorsal tubercles seems to depend at least to some degree on whether the body is contracted (Fig. 1) or expanded (Fig. 2) at the time of fixation. Also the degree of expression of the intrasegmental lines and of the ventrolateral protuberances depends upon the proper preservation of the larva. Because the larva of *lateralis* studied by Michener (1953) was rather poorly preserved, it is believed that these features

<sup>3</sup>Dr. Robbin W. Thorp has kindly sent me the manuscript of his synopsis of the genus *Heterostelis*, in which he briefly describes the larva of a new species. Its mandible is apically bidentate with the lower tooth longer, but lacks an apical concavity. In other respects, it seems to have the general features of megachilid larvae.



FIGS. 11-18. *Stelis (Odontostelis) bilineolata* (Spinola). 11. First instar, lateral view. 12-13. Head of first instar, frontal and lateral views. 14-16. Mandible of first instar, dorsal, adoral, and ventral views. 17-18. Pupa, lateral and dorsal views. Scales refer to Fig. 11 and to Figs. 17 and 18.

would be more pronounced in a fresh specimen and therefore would agree more closely with comparable structures of other known *Stelis* larvae.

On the other hand, the dissimilarities of the mandibles in *Stelis* larvae are striking. The mandibles (Figs. 6-8) are apically bidentate, have serrated apical edges, and an apical concavity in *bilineolata*, *nasuta*, and presumably *ornatula*; they (Michener, 1953, figs. 115, 116) are apically simple and without serrations

or an apical inner concavity in *lateralis* and *minuta*.<sup>4</sup> I know of no other case in bees where two such radically different types of mandibles are encountered in the same genus, and this condition, therefore, suggests the possibility of a polyphyletic origin of the genus.

It is tempting to postulate that the bidentate mandible is associated with a life history in which the parasitic larva does not assassinate the host larva; in this case, the *Stelis* larvae would not require specialized modifications of the mandible to eliminate the host larvae. Consequently, the primitive anthidiine type of mandible persists. On the other hand, as specialized apically simple mandibles have evolved several times in those parasitic anthophorids where the cuckoo bee larva destroys the host egg or larva, we might conclude that this sharp-pointed mandible is similarly employed by these *Stelis*.

There is a certain amount of evidence to support this hypothesis. The larvae of *bilineolata* and *nasuta* do not kill their hosts. The adult of *bilineolata* removes the host larva from the cell (Bennett, 1966) and the larvae of *nasuta*, two to 12 of which occupy a single host cell, apparently efficiently consume the food of the much larger host larva so that it starves (Fabre, 1914). Furthermore, the larvae of both *lateralis* (Graenicher, 1905; Michener, 1955) and *minuta* (Enslin, 1925) (though apparently not as first-stage forms) destroy their host larva with the sharp-pointed mandible.

However, this hypothesis seems to break down when *ornatula* is considered. Both Enslin (1925) and Höppner (1904) have seen its larva attack that of the host and yet Micheli (1935) shows it to have a bidentate mandible with a dorsal serrated edge. The hypothesis should not, however, be totally discarded because it is not clear from Micheli's drawings whether *ornatula*'s mandible is like that of *bilineolata* or whether it is perhaps somewhat intermediate between the two extreme types. It should also be pointed out that Enslin (1925) also examined the larva of *ornatula* and stated that the mature larvae of *minuta*, which has a pointed mandible, and of *ornatula* are "quite similar," a statement which reflects doubt on the correct identification of Micheli's specimen.

#### FIRST INSTAR

(Figs. 11-16)

LENGTH: Approximately 2.5 mm.

HEAD (Figs. 12, 13): Integument without setae, apparently without sensilla, and nonpigmented. Tentorium complete, including thin dorsal arm; posterior thickening of head capsule and hypostomal ridge moderately developed; gena projecting downward so as to cover hypostomal ridge anteriorly; pleurostomal ridge weak but evident; epistomal ridge weak laterad of anterior tentorial pits and absent between them; longitudinal thickening of head capsule, cleavage lines, and parietal bands not evident. Antennal papillae scarcely

<sup>4</sup>This same type of mandible was found on a larva questionably identified as *Stelis punctulatissima* (Kirby) (as *aterrima* (Panzer)) (Hofeneder, 1947). Additional recorded details of the larva are not adequate for comparison with other larvae treated here.



produced. Labral apex emarginate and without tubercles. Mandible (Figs. 14–16) apically bidentate, with scattered minute indistinct denticles along apical edges; apical concavity not defined. Maxilla with apex produced adorally; galea and palpus not evident; cardo and stipes faintly sclerotic. Labium recessed, not divided into prementum and postmentum; salivary opening small and inconspicuous; palpi absent.

BODY: Form (Fig. 11) robust and straight, thickest in posterior half; most segments bearing distinct intrasegmental lines; middorsal tubercles apparently absent; body projecting somewhat on either side below spiracles (in the region of the ventrolateral tubercles of mature larva). Integument without setae but with numerous spicules over most of surface. Spiracles moderately small; atrium apparently without spines or ridges and apparently not projecting above body wall; peritreme distinct; primary tracheal opening with slight collar. Anus dorsal in position.

MATERIAL STUDIED: One larva, Curepe, Trinidad, West Indies, egg deposited February 1–2, larva emerged February 4–5, 1965, in nest of *Euglossa cordata* (Linnaeus) (F. D. Bennett).

Michener (1955) provided some details of the first instar of *Stelis lateralis*. Both species agree in that the straight, robust body protrudes laterally and lacks dorsolateral tubercles. The head is normal in size and the mandibles are not enlarged. Further, there is less difference in the anatomy of the head and mouthparts between the first and last instars of these species than there normally is with parasitic bees.

However, the first-stage forms of the two *Stelis* presumably differ significantly. Whereas the first instar of *bilineolata* has antennal papillae that are much shorter than those of the mature larva, the antennae of the first-stage *lateralis* are longer than those of the last stage. Although setae are not evident on *bilineolata*, setae of *lateralis* are even longer than those of the last larval instar of the same species. As pointed out above, mandibles of the first and last instars of *lateralis* are simple apically and sharp-pointed whereas those of the same stages of *bilineolata* are bidentate.

PUPA  
(Figs. 17, 18)

HEAD: Vertex with three small tubercles in position of ocelli; these tubercles about as pronounced as ocelli of adults; vertex and, to lesser extent, frons and clypeus with pigmented setae.

MESOSOMA: Mesoscutum, mesoscutellum, and axillae with pigmented setae. Coxae and trochanters without spines.

METASOMA: Terga I–VI with bands of pigmented setae.

MATERIAL STUDIED: Four males, Curepe, Trinidad, West Indies, February, 1965, from nest of *Euglossa cordata* (Linnaeus) (F. D. Bennett).

Because the basal mandibular tooth of the female *Odontostelis* is much larger than that of the male, female pupae presumably have a correspondingly larger mandibular tubercle than do male pupae.

The pupa of this species lacks the various tubercles commonly encountered in other bee groups. In this respect it agrees with the pupae of *Megachile* described by Michener (1954) and with the pupa of an unidentified *Dianthidium* kindly loaned by Dr. Paul D. Hurd, Jr., from the California Insect Survey. The pupae of all these megachilids share the apparently unique feature of extensive patches of setae on the head, thoracic nota, and metasomal terga. It would seem, therefore, that the pupae of megachilids, like the larvae (Michener, 1953), are very homogeneous.<sup>5</sup>

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<sup>5</sup> Dr. Robbin Thorp's manuscript account of the pupa of a new species of *Heterostelis* is an exception to this statement in that the pupa is "apparently without long setae on vertex, mesoscutum, and metasomal terga." In contrast with *Odontostelis*, *Heterostelis* possesses only a pair of rounded tubercles on the vertex and a spine on the inner apex of each coxa and on the inner base of each trochanter.